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Forcible Discharge of the Antherozoids in Asterella Californica*

By George J. Peirce

In January, 1901, I had a considerable number of male plants of *Asterella Californica* * on a plate under a bell-glass in the laboratory. The laboratory was moderately warm, the air fairly dry; the soil under the bell-glass was damp, the air moist. On removing the bell-glass to examine the plants more closely, I was presently surprised to see slight puffs of what looked like smoke coming from the sods. I scrutinized the material thinking there must be a puff-ball in it, but could see none. On the contrary, the little puffs of smoke came from different places over the plate and, on looking carefully, I thought they must come from the groups of antheridia. I held a glass slide over the plate, caught a puff or two on it, and examined it under the microscope. What I saw were great numbers of the antherozoids of this liverwort sticking to what had been the lower surface of the slide. I tried this again several times with the same result—the antherozoids were forcibly projected above the surface of the plant. The slides were held from five to ten centimeters above the plants, but I made no exact measurements at that time, for I was not sure that what I had seen was not a wholly unusual phenomenon, possible only under the unnatural conditions prevailing in the laboratory. The plants had been in the laboratory for some time—two weeks, possibly longer—on a table six feet from the window. They were average plants when I brought them in, but they had not developed in the laboratory so fast as plants which I had left undisturbed out of doors. It was impossible for me to test the plants out of doors for they were already too old to discharge any more antherozoids, so I was obliged to stop work on the matter for this reason.

From Professor D. H. Campbell, of this university, and Dr. M. A. Howe, of Columbia University, I learned that what I had seen was new, not hitherto recorded in the literature with which they are familiar and which is quite unknown to me, and I determined to watch the plants out of doors as well as in the laboratory during the following season.

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* This plant has also been known as *Fimbriaria Californica.*

On January 20 of this year (1902) I thought the plants of *Asterella Californica* were in proper condition for testing whether they do or do not discharge their antherozoids under the conditions prevailing out of doors, and I set some glass slides to catch antherozoids if any should be expelled. A word may be said as to the weather and the place, as well as the manner and the result, of my experiment. The rains came early this season, in October and November, the season being ahead of the average when December began. There was no more rain to speak of till January 18. On December 11 the weather became decidedly cooler and remained cool, with frequent white frosts at night for weeks. There have been heavy dews and heavy fogs at night, some of the fogs being so heavy as to wet the streets enough to make the surface sticky. The days had been sunny as a rule, but there had been little growth and development among plants. In consequence, *Asterella* is not so far along as usual at this time. The bank where *Asterella* grows is sandy, steep, more or less covered with grass, shrubbery, mosses and liverworts, about half a mile from this university, and faces northeast, receiving little direct sunshine. On the morning of January 18 I was struck by the dryness of the soil there compared with last year. We had 20 mm. of rain the following afternoon and night; the sun shone brightly and the air was warm on the 19th. The plants were then in perfectly normal, healthy condition on the morning of the 20th, after a night of heavy dew and comparative mildness.

The sun was shining brightly, the air was rapidly growing warmer, as I set my slides at various distances from male plants of *Asterella*. The slides had been cleaned and numbered, and were held in place by wire holders thrust into the soil. The slides did not touch the plants and were in various positions, some horizontal, others oblique or vertical, corresponding to the positions of the plants. Slide no. 1 was 2–3 cm. from a patch of young *Asterella* growing on a vertical part of the bank. Other slides were nearer, others much further from the plants, from 0.5 cm. to 15 cm. I put out the first slides at 10.15 a. m., the last one at 11. At 4.30 p. m. I took a microscope out to the bank and looked at some of the slides, but it was too late to examine all and the light was uncertain at best. Slide no. 1 had some dead antherozoids sticking to it. I did not see any on the other five slides examined. I put no. 1 back and brought the other five with me for more careful examination in the laboratory. The day had been warm and sunny, the air was much dryer during the day than at night, and there was some breeze throughout the day (a circumstance which might account for there being no antherozoids on any slides except no. 1). By seven o'clock in the evening it had begun to rain, and it rained gently for three hours.

There was white frost on the lowlands on the morning of January 21, but none on my bank. At 9.30 I took a microscope out again. Slide no. 1 had water on it, making a ridge along the lower edge on the side next the bank. I carefully took the slide out of the wire holder, turned it flat so that the water spread over the upper surface, and put it on the microscope. There were *Asterella* antherozoids in considerable numbers—a dozen in one field of Leitz objective VI and ocular 3—swimming about in the water. These antherozoids could have come upon the slide only as did those dead ones found on it the afternoon before, by being forcibly projected from the antheridia imbedded in the plants. It is evident, then, that the antherozoids are expelled when the plant is under perfectly natural conditions, and that what I saw a year ago was not a laboratory phenomenon merely.

From the conditions prevailing when I first saw the expulsion of these antherozoids, I thought the mechanics of the process might be as follows: that the walls of the antheridia and the adjacent tissues of the plant give up water in comparatively dry air faster than the contents of the antheridium can; that pressure develops which finally exceeds the resistance of the wall of the antheridium; that this breaks suddenly and the antherozoids are thus thrown out through the openings of the cavities in which the antheridia lie. This hypothesis seemed to be strengthened by my finding antherozoids in the afternoon, after a day of comparative dryness following a night when the dew was heavy. But the occurrence of antherozoids on the slide which was out all night and during a rain does not favor this view. The number of antherozoids on this was decidedly larger, perhaps because the time of exposure was longer (about three times as long), perhaps because the antherozoids did not fall off the wet slide as they might from a dry one, perhaps because the breeze was gentler or different in direction, etc. The main thing is the occurrence of antherozoids on the slide under two sets of conditions very different from each other. The mechanics of expulsion cannot be such as I at first thought.

Having proved that *Asterella* expels its antherozoids out of doors under natural conditions and not merely in the laboratory, I decided to bring plants in for further study. So many things may act as disturbing influences out of doors—the wind, rain, animals, etc.—that no satisfactory tests of the distances to which the antherozoids may be thrown are likely to be made out of doors without a great expenditure of time and trouble. I brought a considerable number of male plants of somewhat different ages into the laboratory, arranged them on a plate, fastened to the edge of the plate wires holding slides at different heights above the plants, and covered the whole with a bell-glass, first taking care that the plants were thoroughly wet. On the afternoon of the following day I found a few antherozoids on one slide about seven centimeters above the plants. On the morning of the next day but one there were grayish spots on three slides, five to seven centimeters above the plants. These spots I feared were excrementitious matters from some insect but proved on examination to be extensive masses of antherozoids in the slime in which they are discharged. This slime consists presumably of the gelatinized walls of the mother-cells of the antherozoids together with whatever protoplasmic matters remain and degenerate in the mother-cells. The slime is very important in contributing to the expulsion of the antherozoids.

I put the slides on higher holders and waited another twenty-four hours, again watering the plants before putting the bell-glass over them. Much to my astonishment, on the following morning, one of the slides, fourteen centimeters above the plants, had a series of spots on it as shown in *Fig. 1.* This figure is a tracing, moderately exact as to the shape and size of the spots and exact as to their number and arrangement, made on thin paper from the stained preparation on the slide. These spots certainly suggest fly-specks, but examination with the microscope proves them to be masses of antherozoids. I again put fresh slides on holders still higher, but I caught no antherozoids on these highest slides. Any one of these possibilities may account for this, namely: the plants may have stopped forming antheridia and have emptied all those already made, or none may have been ready to burst while the slides were up, or the slides may have been between instead of in the path of expelled antherozoids, or the slides may have been just too high to catch any. Certainly the antherozoids caught on the slide fourteen centimeters above the plants would have gone considerably higher if they had not been caught. The highest slides I put in place were about 21 cm. above the plants. One may say, then, that *Asterella* can throw its antherozoids, under favorable conditions, to a vertical height of 14–20 cm.

The spots made on the slide by the discharged antherozoids are dense or thin, close together or scattered, according as the slide receives the discharge from the antheridium before or after the discharge spreads out. The outlines of the spots represent cross-sections of the discharge at the height of the slide. In *Fig. 1* there are so many spots that two or three plants must have discharged their antherozoids upon the one slide. The outlines of the spots even under the microscope are very sharp, the antherozoids are held together in very compact masses, the slime serving as the matrix. On some slides, instead of such dense spots, there is an immensely larger number of smaller spots, visible only under the microscope. These spots consist (*Fig. 2*) of a considerable number of antherozoids in a thin layer of slime. The slime layer varies somewhat in thickness in different parts of the spot. From my slides it is obvious that the antherozoids are discharged while enclosed in slime, that the main mass of slime breaks up during its flight into smaller ones, these again dividing perhaps, and that finally the antherozoids fall again to the ground in little groups, the enclosing slime dissolving in the dew or rain, on the surface on which they fall, thus liberating the antherozoids. The antherozoids thereupon swim off, swimming then for the first time although they may have been carried far on the breeze which also helped to break up the discharge from the antheridium. The slime, holding the antherozoids together in little groups, is distinctly beneficial in so doing. It is a protection, besides, in keeping the antherozoids from drying and stiffening, as such minute bodies would surely do unless enclosed in a matrix which holds water more effectively than protoplasm. That there is always slime about the antherozoids till they fall on a wet surface is shown by my dry slides. That the slime dissolves, thus liberating the antherozoids, which thereupon swim away, is shown by my wet slide out of doors.

Antherozoids on the slide, whether singly or in patches, may be fixed and stained by the methods applied to staining cover-glass preparations of bacteria. I tried several methods, of which Fischer's * for staining cilia was the most successful. Of course, this method is not recommended for the cytological study of the antherozoids. I recommend it only for the purpose of demonstrating perfect antherozoids, ciliated and enclosed in thin slime, which have been caught on slides.

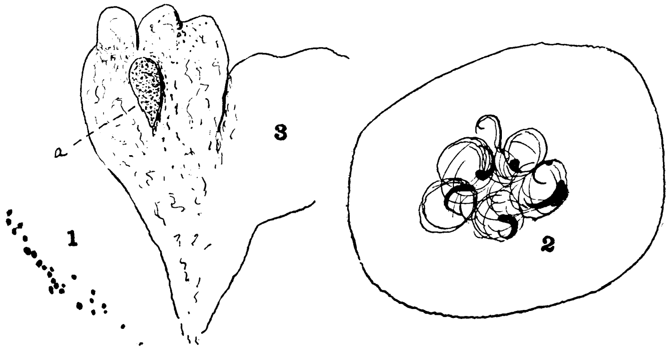

FIG. 1. A tracing of spots formed on slide by discharge of antherozoids from antheridia 14 cm. below.

FIG. 2. A very small spot, showing ciliated antherozoids and slime in which they are imbedded, × 755. Leitz drawing-prism.

FIG. 3. Sketch of male plant of *Asterella Californica*, showing cushion (*a*) in which antheridia develop, × 3.

We come back now to the mechanics of expulsion. The discharges which I have seen take place or have caught on the slides, have occurred only when the soil and the plants were full of water. Not only the tissues of the antheridia, but the surrounding vegetative tissues were turgid. Given an abundant supply of water in the soil, turgidity will always develop. The structure of these turgid parts demands a moment's notice. The antheridial patches of *Asterella*, as shown in *fig. 3*, are somewhat raised above the general surface of the thallus. The tissue composing and underlying this elevation is very different from that elsewhere. A section through one of these antheridial patches parallel with and below the surface of the thallus, shows that the thallus is composed in the main of moderate sized cells, containing many chlorophyll grains and with small intercellular spaces between, while the part of the thallus where the antheridia are consists of much larger cells, with far fewer chlorophyll grains, cell-walls no thicker, and (when the tissue is full of water) there are no intercellular spaces. The distribution of these tissues is plain to the naked eye, for the part under or among the antheridia appears quite colorless compared to the adjacent tissue rich in chlorophyll. *Fig. 4* shows such a section. The part of the section outside the bounding line consists of chlorophyll-containing rather small-celled tissue. Within the line one sees holes of various sizes and shapes between which are comparatively large, thin-walled cells pressed close together owing to their turgidity. (I sectioned a thallus from very wet soil.) In the spaces *a* and *b* were antheridia, in the other spaces there were none. Some of these spaces are nearly obliterated, as those lettered *c* and *d* show. *Fig. 5* is an enlarged drawing of the part *a* of *fig. 4*, that is, a cross section of an antheridium enclosed in the turgescent nearly colorless tissue of the cushion. The cells forming the wall of the antheridium are shown in outline (*a*), the adjacent and closely pressing vegetative cells are only partly shown (*b*), while the blank central portion (*c*) represents the mass of antherozoids enclosed in slime, forming the greater part of the antheridium. *Fig. 6* is a longitudinal section of an antheridium, a section at right angles to the surface of the thallus, similarly lettered. All the sections are free hand, and the one shown in *fig. 6* does not show in quite true proportions the opening of the chamber in which the antheridium lies. The tissue within the bracket *d* is composed of comparatively small cells, rich in chlorophyll, the tissue bracketed *e* is composed of large cells, comparatively poor in chlorophyll, and capable of great changes in volume. It is precisely this comparatively colorless tissue in which the antheridia are imbedded which furnishes much of the force by which the antherozoids are ejected.

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* Jahrb. wiss. Bot. 27 : 82. 1895.

The mechanism effecting the ejaculation of the antherozoids consists of two parts—*first*, of the shiny, water-absorbing matrix consisting of gelatinized mother-cells and thin walls, in which the antherozoids lie and which fills and distends the ripe antheridium still enclosed by the single layer of peripheral cells; *second*, the thin-walled, large-celled, water-absorbing tissue composing the cushion, in chambers of which the antheridia develop. These two, the tissue and the slime, expand in opposite directions as they absorb water, the one tending to decrease, the other to increase, the size of the chambers containing antheridia. The two pressures would tend to offset each other and would affect nothing if they met on all sides of the antheridia. The chambers in which these lie, however, are open above and are covered by the chlorophyll-containing, smaller-celled, and more rigid tissue indicated by *d* in *fig. 6*. Hence the antheridia are distended in all directions, upward as well as otherwise, and are compressed from all sides, *except from above*. The distending and compressing strains finally result, under these considerations, in the rupture

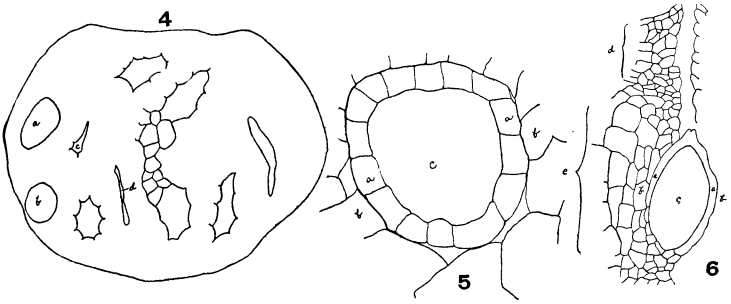

FIG. 4. Section through cushion, parallel to and below surface of thallus, showing cavities containing antheridia (*a* and *b*), empty cavities, and cavities nearly obliterated (*c* and *d*) by pressure of the thin-walled cells composing cushion, × 22.

FIG. 5. Enlarged drawing of *a* in *fig. 4*, × 172.

FIG. 6. Section through antheridium at right angles to surface of thallus, × 172. The lettering in *figs. 5 and 6* denotes: *a*, wall of antheridium; *b*, turgid cushion-tissue compressing antheridium; *c*, mass of antherozoids in slime composed of degenerated walls and contents of mother-cells. This absorbs water and distends antheridium; *d*, solid chlorophyll-containing tissue, with opening of chamber; *e*, water-absorbing turgescent cushion-tissue. The figures were drawn with Leitz drawing-prism.

of the antheridium and the discharge of its contents through the mouth of the chamber, the total force expanding itself all in one direction with the astonishing result just described.

The distance to which antherozoids will be thrown will depend on the one hand upon the turgidity of the antheridia and of the vegetative parts of the plant, and on the other hand upon the position of the plant and upon the wind. The antherozoids may be thrown violently against nearby objects, leaves, branches, etc., when the force was sufficient to have carried them much farther if the plants had only been growing in more open places. But the main external influences are wind and water. The wind may blow the antherozoids back upon the parent plant or take them far away, dropping them near female plants or scattering them where there are none. When the antherozoids fall to the ground they must swim the rest of the way if they are to accomplish their purpose. An enormous number of antherozoids are discharged from each antheridium, and there are several or many antheridia on each male plant. Without counting at all, I should say that there appear to be about equal numbers of male and female plants, and that the number of archegonia is about the same as the number of antheridia. At all events the number of antherozoids enormously exceeds the number of egg-cells. Since these plants are dioecious, cross fertilization is all that is possible. But what does the plant pay for this? The dioecism of this species is coupled with the forcible discharge of the male elements. These may or may not be transported by this means nearer to the female elements which they must reach by swimming and with which they must fuse if they are to be useful.

It would be interesting to know whether other dioecious liverworts have this same habit. I hope next year to test other plants for this phenomenon, but I do not wish by this statement to reserve the field to myself.

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